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# BIOLOGICAL BULLETIN

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## OBSERVATIONS ON THE DEVELOPMENT OF COPIDOSOMA GELECHIAE.

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*From the Marine Biological Laboratory, and the Zoological Laboratory of the University of Texas (Contribution No. 127).*

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### I. INTRODUCTION.

The discovery of polyembryonic development among certain of the hymenopterous parasites has opened up an extremely interesting field for investigation. Like most other important biological discoveries, this one was foreshadowed by the observations of several different naturalists. In a paper of this nature it is not necessary to give an extended account of the history of this discovery. We shall therefore be content with a brief

statement on this point, limiting the account almost entirely to the species with which the paper deals.

The general features of polyembryony in insects have been given in the well-known papers of Marchal ('98, '04) and Silverstri ('06, '08), but there are many points concerning the details of this process which have not as yet been worked out. It was with the view of studying certain of these details that led the writer three years ago to seek an American species upon which such studies could be made. Dr. L. O. Howard<sup>1</sup> suggested that *Copidosoma gelechiæ*, which parasitizes the larvæ of the *Solidago* gall moth, *Gnorimoschema gallæsolidaginis*, would be a good form upon which to work, as it seemed to be an undoubted case of polyembryony.

The *Gnorimoschema* moth makes the ellipsoidal galls on the stems of several species of goldenrod. Baron Osten Sacken ('63) seems to have been the first to have published a description of the inflated carcass of the *Gnorimoschema* larva, caused by the chalcis parasite; but apparently he was not acquainted with the maker of the gall. In 1869 in connection with his account on the life history of this moth, Riley states that the caterpillar serves as a host for no less than six different species of hymenopterous parasites. One of these, which is shown in his Fig. 6, Plate 2, is described as a "little fly of a dark metallic green color, with reddish legs." This is clearly *Copidosoma*. Riley states that the larvæ of this species infests the caterpillar in great numbers, more than 150 having been obtained from a single host. He supposed that the "mother fly" gnawed a passage through the gall and desposited her batch of eggs in the inmate. He pointed out that the larval parasites cause the caterpillar to swell to three or four times its natural size, and after having absorbed all the juices of the victim, form very small brownish cocoons, which are so packed together that they give to the worm the puffed-up appearance which is typical of the mummified carcasses of lepidopterous larvæ that have been parasitized by a polyembryonic species. It was this inflated condition of the larval host that led Riley to call the parasite the "Inflating Chalcis

<sup>1</sup> For this as well as for other suggestions received throughout the progress of the work, the writer is greatly indebted to Dr. Howard.

Fly." Howard ('85) later named this species *Copidosoma gelechiæ*.

Upon examining the various goldenrods about Woods Hole, Mass., for galls of *Gnorimoschema*, it was found that *Solidago sempervirens* furnished the best opportunity for obtaining material. However, the common gall maker of this solidago proved not to be *Gnorimoschema gallæsolidaginis* Riley, but a closely related species, *G. salinaris* Busck. The parasites infesting these two moths are varieties of the same species, *Copidosoma gelechiæ*.

The selection of this species has not proved altogether satisfactory, because the gall-making habit of the host complicates the life history and renders the collecting of material for early stages of the parasite somewhat more difficult than from a host which feeds openly. Furthermore, the moth, and likewise the parasite, has but one generation a year. In addition to these objections, there is the further one that the egg of *Copidosoma* gives rise to a relatively large number of individuals (about 191 on the average). In attempting to obtain material for the studies which the writer has in mind, it seems best to seek to find a host which is an open or semi-open feeder, which has two or more generations a year, and which harbors a parasitic egg giving rise to but few individuals. During the past summer at least two species have been found which in the main seem to fulfill these conditions. It therefore seems best to publish the main facts concerning the development of *Copidosoma* before giving it up for more favorable material.

There is one feature in the development of *Copidosoma* which makes further study desirable. We refer to the abortive embryos (presently to be described), which at first were thought to be comparable to the so-called asexual larvæ of *Litomastix truncatellus*. It will be recalled that Silvestri ('06) described in this species the development of both sexual and asexual larvæ from a single egg. In one instance he secured from a caterpillar of *Plusia gamma* 1,700 sexual and 220 asexual larvæ of *Litomastix*. He believes that the asexual larvæ play the rôle of rasps for the normal larvæ, tearing the tissues of the host so that the sexual larvæ may the more easily secure the necessary food. It may

be stated here that the abortive larvæ of *Copidosoma* are in no way comparable to the asexual larvæ of *Litomastix* as described by Silvestri.

## II. NOTE ON THE LIFE HISTORY OF GNORIMOSCHEMA.

In order to collect polyembryonic material it is essential to know something about the life history of the host; especially is this true in cases like *Gnorimoschema* in which the larval host is a gall maker. Considerable attention has therefore been given to a study of the life history of *G. salinaris*.

The general habits of the *Solidago* gall moths were first made known by Riley's ('69) studies on *G. gallæsolidaginis*. According to Riley this species winters over in the imago stage and may be seen flying in the month of May. When the young plants (*Solidago nemoralis*) are about six inches high the female moth lays her egg either in the terminal bud or at the side of the stalk immediately below the bud. The young caterpillar upon hatching burrows into the stalk and starts the development of the gall. By the first of June the gall has just begun to form and contains a larva about one-third grown. The larva and its ellipsoidal gall reach their full size by the middle of July. The caterpillar which now measures over half an inch in length prepares for the change into the chrysalis state by first eating a round passage-way through the wall well toward the upper end of the gall. The orifice is then closed by a secretion of liquid silk, which hardens to form a silken plug. After closing the orifice, the caterpillar lines the passage-way and the walls with a delicate silk, and then transforms into a shiny, mahogany-brown pupa, about a half inch long. The moths begin to emerge about the middle of August and continue to appear until the beginning of October.

Many phases of the life history of *G. salinaris* are similar to those of *G. gallæsolidaginis*, but there are some important differences. The earliest date at which galls of the marsh goldenrod have been secured was June 12, 1914, and at that time many of the galls were well started. Between June 12 and 15, 63 galls of various sizes were collected and examined. They varied in size from 8 to 12 mm. in length and from 4 to 17 mm. in transverse section. In shape the galls also vary greatly. Some are distinctly

pear-shaped, while others are fusiform, with various gradations between these two general types. The galls occur at different heights on the stem, but the vast majority of them are located at or near the base of the stalk (Fig. 1). Their position is undoubtedly determined by the location of the point at which the larva penetrates the young shoot. If this point is located toward the base of the young stalk, the gall will naturally appear near the base of the fully grown plant; but if it is located in or near the terminal bud, the gall will appear some little distance up on the stem. Occasionally two galls are found on the same plant (Fig. 8). A few cases have been observed in which the gall was located at the tip of the terminal bud, producing a stunted plant without a central, flower-bearing stalk. With these few exceptions, the gall of *G. salinaris* does not seem materially to affect the growth and vigor of the plant. It is true that many galls are found on plants that are apparently stunted but such dwarfing is to be attributed to the adverse conditions under which the plant sometimes grows. In regions that are very much exposed to the wind, like the banks along the coast, many of the goldenrods are small and clearly dwarfed; but this condition applies as well to the plants that are free from galls as to those that are infected.

The habits of gall making are similar in the three common species of *Gnorimoschema*, although the following differences may be pointed out. *G. gallæasteriella* produces a triangular gall at the top of the dwarfed or stunted stems of *Solidago cæsia*, *S. axillaris*, *S. latifolis*, and *Aster divaricatus*.<sup>1</sup> The form of the gall differs somewhat with the plant. The gall of *G. gallæsolidaginis* may occur toward the top of the stem, but usually it is located just below the middle, especially is this true of the galls on *S. canadensis*. The galls of this moth do not dwarf the plant. The condition of the galls of *G. salinaris* on the marsh goldenrod has already been described. They occur nearer the base of the stem than do those of last species, and like the latter there is little or no tendency to dwarfing the plant.

The larvæ secured from the galls collected between June 12 and 15 varied from 3 to 8 mm. in length. Beginning with the middle of June, the young caterpillars grow rapidly, doubling

<sup>1</sup> Part of these data were kindly furnished the writer by Dr. T. M. Forbes.

their size within a fortnight. By the middle of July they have reached their full growth, and are beginning to show signs of undergoing pupation, which is evidenced by the construction of the passage-way. The passage-way and its orifice differ in two respects from those of *G. gallæsolidaginis* as described by Riley ('69). The silk lining does not extend much beyond the lower limits of the passage-way, and hence does not cover the inner surface of the wall. The second difference is seen in the character of the orifice and its silk plug. The caterpillar of *G. salinaris* does not cut the passage-way quite through the wall, but leaves the very thin epidermis of the stem, which is used as a background for the construction of the plug (Fig. 7).

TABLE I.

TABLE SHOWING DATES OF PUPATION AND EMERGENCE OF COPIDOSOMA AND GNORIMOSCHEMA.

Pupation (Beginning of)	Copidosoma	<ul style="list-style-type: none"> <li>Aug. 6, 1912.</li> <li>Aug. 5, 1913.</li> <li>July 31, 1914.</li> <li>July 30, 1915.</li> </ul>
	Gnorimoschema	<ul style="list-style-type: none"> <li>Aug. 6, 1912.</li> <li>July 23, 1913.</li> <li>July 30, 1914.</li> <li>July 26, 1915.</li> </ul>
Emergence	Copidosoma	<ul style="list-style-type: none"> <li>Aug. 25 to Sept. 12, 1912.</li> <li>Sept. 3 to Sept. 13, 1913.</li> <li>Aug. 30 to Sept. 18, 1914.</li> <li>Aug. 24 to Sept. 21, 1915.</li> </ul>
	Gnorimoschema	<ul style="list-style-type: none"> <li>Aug. 25 to Sept. 10, 1912.</li> <li>Aug. 25 to Sept. 10, 1913.</li> <li>Aug. 22 to Sept. 11, 1914.</li> <li>Aug. 24 to Sept. 14, 1915.</li> </ul>

Pupation occurs during the last week of July and the first week of August (Table I.). The imagines begin to emerge about August 25, and continue to appear until September 10. The moth has been seen flying in the open during this period.

Females kept in captivity often lay eggs. This they do within ten days after emerging, and irrespective of their association with males. As a rule the moths simply drop the eggs on the bottom of the cage, or they may lay them on the leaves and flowers of goldenrods placed in the cage. At first it was thought that *G. salinaris* must differ from *G. gallæsolidaginis* in respect to its egg-laying habits, for Riley states that the latter species although emerging in the fall, hibernates as an imago and lays

its eggs in the following May. It has been discovered, however, that *G. gallæsolidaginis* from the galls of *S. canadensis* in western Ohio likewise drops several eggs soon after emerging from the pupa in September. This raises the question as to whether these fall eggs develop into larvæ, for if so it would be difficult to explain how the young caterpillars could withstand the winter and succeed in the spring in finding a young goldenrod bud or shoot in which to start the new gall.

In reply to an inquiry, Mr. A. Busck of Washington kindly informed the writer that the laying of eggs by *Gnorimoschema* was of no particular significance, as it is not uncommon for certain Lepidoptera to drop their eggs prematurely, especially if kept in captivity. In view of this fact an observation made in the fall of 1913 is of special interest. During the first few days of September of that year a single female, confined in a cage with several males, laid a dozen or more eggs on goldenrod leaves and flowers. On the thirteenth of the month three larvæ hatched from this batch of eggs! There can be no possible doubt as to the correctness of this observation, for the hatching of one of the little caterpillars was actually observed under a hand lens.

It is difficult to explain the development of these larvæ from fall eggs, except on the basis of parthenogenesis. It is true that the female which laid the eggs from which the larvæ developed had been confined with males; but although males and females have been kept together for several weeks during each of the last three seasons, yet mating has never been observed. The supposition that the fall eggs of *G. salinaris* may develop by parthenogenesis receives strong support from a study of sections of eggs laid by a female not associated with males. In Fig. 20 is shown a transverse section of one of her eggs and it can clearly be seen that development is well started. Twelve eggs out of the batch were sectioned, and it was found that eleven had started to develop, although apparently not in a normal manner. It is not improbable that some few eggs may develop normally and eventually produce larvæ. The question of parthenogenesis in the *Solidago* moths is one needing further study.

It might be worth while to add that parthenogenetic development among Lepidoptera is by no means unknown. DeGeer is



given credit for having first discovered long ago that certain butterflies belonging to the genus *Solenobia* lay unfertilized eggs which develop into normal imagines, and later von Siebold not only confirmed this observation, but also discovered that *Psyche helix* reproduced parthenogenetically. It has since been shown by several workers that the silk moth, *Bombyx mori*, may under certain conditions reproduce by parthenogenesis.

### III. PARASITES OF GNORIMOSCHEMA SALINARIS.

Riley reports six hymenopterous parasites for *Gnorimoschema gallæsolidaginis*, and in addition to these he found a beetle larva and another lepidopterous larva which intrude as inquilines within the cavity of the gall made by this species. At least five hymenopterous parasites have been found associated with *G. salinaris*. The most important of these is *Copidosoma gelechiæ*, which is by far the most common parasite attacking the moth. The other four species are *Calliephialtes notanda* Cress, *Epiurus* sp., *Eurytoma* sp. (pupa), and *Pseudacrias sexdentatus* Girault. The first of these four occurs most frequently, while the last has been observed but a few times. However, it is of special interest, inasmuch as it is the only observed case of a second parasite emerging along with *Copidosoma*, although the larvæ of other species have been found associated with the larvæ of *Copidosoma*. On September 3, 1914, six individuals, all females, emerged together with a brood of about one hundred *Copidosomas* from a single carcass. The small pupæ of *Pseudacrias* lying among those of *Copidosoma* were observed through the transparent chitin of the carcass of the host some days prior to their emergence. They were not grouped together but scattered about in different parts of the carcass. Each pupa was inclosed in a chamber very much smaller than, but exactly similar to that containing a *Copidosoma* pupa.

Usually *Pseudacrias* larvæ do not pupate until after the larval host has undergone this process. About a dozen *Gnorimoschema* pupæ have been found containing *Pseudacrias* pupæ, which later emerged. It is not probable that *Pseudacrias* is polyembryonic. First, because both male and female individuals usually emerge from the same pupal host; and second, because the individuals

do not come out at the same time. The single instance of six females issuing simultaneously with the brood of *Copidosoma* can be explained by assuming that a single female deposited six fertilized eggs in the host at the same time. However, this case is of special interest as it demonstrates the synchronous development in a single host of the broods of two distinct parasites, and thus supports Wheeler's ('10) suggested explanation of Silvestri's so-called asexual larvæ in *Litomastix*.

In addition to the five hymenopterous parasites, there are two insect larvæ associated with the larva of *G. salinaris*. They are undoubtedly inquilines. One of these is a beetle and the other a lepidopterous larva (Fig. 5). Judging from Riley's account, these two species are very similar to if not identical with the corresponding inquilines reported by him for the galls of *G. gallæ-solidaginis*.

#### IV. DEVELOPMENT OF COPIDOSOMA GELECHIAE.

##### 1. *The Polygerm Stages.*

(a) *Youngest Stages.*—We have not secured the cleavage stages of *Copidosoma*, owing to the fact that they occur earlier in the year than we have been able to reach Woods Hole. Therefore, in describing the developmental processes which have their inception in the cleavage stages, we must rely upon the work of other investigators in this field for our interpretation of the significance of these processes.

The youngest stages secured were found in a small larva of *Gnorimoschema*, taken June 21, 1913. The series of sections of this small caterpillar contains three young polygerms of *Copidosoma*. Evidently the egg from which the caterpillar developed had had three parasitic eggs deposited in it. Two of the polygerms, which lie close together, are situated in the first and second body segments of the larva, just beneath the hypodermis; while the third is found in sections 5 to 14 posterior to these, and is also situated just beneath the hypodermis of the host.

The three polygerms are not of the same size, as is indicated by the following measurements: Of the two specimens lying close together, the larger measures  $150\ \mu$  by  $82\ \mu$  and runs through 15 sections ( $150\ \mu$ ), the smaller measures  $103\ \mu$  by  $71\ \mu$ , and is

found in 12 sections; the single specimen measures  $179\ \mu$  by  $95\ \mu$  and occupies 8 sections only.

In structure the three polygerms are practically identical. Each consists of two distinct zones: (1) An outer relatively thick zone containing a large number of nuclei irregularly placed, and (2) a central region containing the embryonic nuclei (Fig. 19). In the absence of the earlier stages, it is not an easy matter to interpret the conditions seen in these polygerms. In the main they correspond most nearly to the conditions in the egg of *Litomastix* (*Copidosoma*) *truncatellus*, as described by Silvestri ('06). I therefore interpret the outer zone to be the product of the "polar oöplasm" plus the "polar nuclei," while the central region contains the true embryonic nuclei, derived from the fertilized nucleus, or in the case of parthenogenetic development, from the matured egg nucleus.

There is of course one essential difference in the corresponding stages of *Litomastix* and *Copidosoma*. In the polygerm of the former the central region is composed of a solid mass consisting of distinct cells, while in the latter this region is on the point of being broken into multi-nucleated masses, which form the primordia of the embryos (cf. Fig. 19 *A* with Silvestri's Fig. 33, Pl. III.). It may be that the embryonic nuclei are delimited by cell walls in *Copidosoma*, although one can not make them out with certainty, even under the highest powers of the microscope. Judging from the work of other investigators, one would expect to find the embryonic nuclei surrounded by cell walls. In *Ageniaspis*, Marchal ('04) first reported that the early embryonal masses were pluri-nuclear in character, but Silvestri ('08) and Martin ('14) have later demonstrated that the nuclei are surrounded by cell walls. In *Copidosoma* the embryonic nuclei are often so closely packed together that the demonstration of cell walls would be extremely difficult.

The three polygerms mentioned above are of particular interest, in that they show very clearly the manner in which the central mass with its nuclei breaks up to form the primordia of the multiple embryos. The central region itself consists of two distinct substances. (1) A granular protoplasm in which the embryonic nuclei lie, and (2) a more fluid-like material which

becomes greatly shrunken during the process of fixation, and which in sections appears as a precipitated substance (Fig. 19 *A*, *P.M.*). As to the origin of these different substances we know nothing, but their subsequent history is clear. For the sake of clearness in description we shall use the following terms: (1) *Nucleated Membrane* for the outer zone; (2) *Granular Layer* for the protoplasm containing the embryonic nuclei; and (3) *Precipitated Material* for the shrunken fluid-like substance.

(b) *The Nucleated Membrane*.—In these young polygerms the outer zone stains more deeply than the central mass. The “polar nuclei” have no definite arrangement, but are irregularly scattered throughout the protoplasm. The entire zone therefore is in every sense of the word a syncytium. As the polygerm grows in size the nuclei become arranged into a single layer, and the protoplasm thins out, thus forming a true nucleated membrane about the central or embryonic portion of the egg (Fig. 21, *N.M.*). In the later history of the polygerm some of the nuclei are clearly surrounded by cell walls, that is, there is a tendency for the membrane to become cellular.

At first the young polygerms are naked, that is there are no elements from the host tissue laid down on the outer surface of the nucleated membrane. Later a few mesenchyme cells are found on the surface of the membrane, and still later these cells give rise to the adipose tissue (Fig. 22, *A.T.*), which may completely surround the polygerm.

(c) *Precipitated Material*.—This material occupies the central portion of the polygerm. Apparently it is formed through the action of the fixing reagent upon the fluid-like protoplasm. In sections it is very much shrunken, thus leaving an irregular clear space (Fig. 21, *C*). As we shall see later, it persists throughout the entire polygerm phase of development.

(d) *The Granular Protoplasm and the Embryonic Nuclei*.—In Fig. 19 the condition of the embryonic nuclei and their surrounding granular protoplasm is especially clear. Most of the nuclei are indifferently scattered in the protoplasm, but some of them are collecting into groups. The number of nuclei in each group is variable; some groups contain only two or three nuclei, while others may have as many as ten or twelve. The granular pro-

toplasm surrounding a group of nuclei soon rounds off and the primordial embryo with its surrounding layer lies free within the more fluid contents of the central region of the egg (Fig. 19 *A*). The more usual condition is for the spherical mass to remain attached at one side to the peripheral layer of the granular protoplasm (Fig. 19 *B*, *P.E.*). Eventually all of the embryonic nuclei thus become included in these spherical masses of protoplasm, and thus become isolated as primordia of the embryos.

The condition at the close of the formation of the primordia is shown in Fig. 21. This specimen was found in a series of sections of a 3 mm. caterpillar, taken June 15, 1914. In the median section it measures  $113\ \mu$  by  $203\ \mu$ , and runs through 40 sections ( $280\ \mu$ ). It lies in the middle portion of the body cavity, to one side of the intestine, which on account of the size of the polygerm is pushed out of place. As compared with the preceding polygerms this one is very much larger and shows a number of important changes. The nucleated membrane has become much thinner and its nuclei are arranged more or less into a single layer. The adipose tissue is being laid down on the outer surface of the membrane. The most important change, however, has occurred in the embryonic masses themselves. The protoplasm which surrounds a group of nuclei is differentiated into two distinct regions. The central part, crowded with nuclei, stains somewhat lighter than the peripheral zone, which forms a relatively dense layer about the central core (Fig. 21, *P.E.*). There are still a few nuclei which have not as yet been surrounded by the dense layer, but this stage marks approximately the end of the division of the germ into separate embryos.

(e) *Growth of the Polygerm and the Formation of the Primary Divisions or Masses.*—Upon the completion of the primitive embryos, the polygerm grows very rapidly. It first extends in the direction of its long axis, soon transforming into an elongated cylindrical structure. One specimen showing this condition measures in section  $148\ \mu$  by  $430\ \mu$ . It never becomes an elongated tube as does the polygerm of *Ageniaspis*. During this growth the adipose tissue is laid down in the form of a thick layer about the polygerm. One of the easiest ways in which to find a polygerm of this and later stages is to examine the large

fat bodies lying in the middle region of the body cavity of the larval host. If the caterpillar is parasitized one of these bodies is almost certain to contain the polygerm.

After the elongated condition is attained, the further growth of the polygerm may take place in any direction. In some cases the extension is mainly in one plane, thus transforming the polygerm into a flat, plate-like structure (Fig. 13). In other cases it forms a thick irregular mass (Fig. 11), and when viewed as a whole mount shows many elevations on its surface, due to the breaking up of the entire polygerm into single masses, each of which contains an embryo.

During the rapid expansion of the polygerm a very important change takes place in its structure, whereby each embryo become enclosed in a double involucre. The first step in this process begins just prior to that period of development in which the polygerm attains its elongated, cylindrical shape. It consists in the formation of constrictions in the nucleated membrane which break up the single polygerm into a series of primary divisions or masses (Fig. 15). In the specimen shown in this figure there are about twelve of these masses. Each primary mass has the same general structure as the original single polygerm. It is surrounded by a portion of the nucleated membrane, contains precipitated material, and has a variable number of embryos, from five to fifteen or more.

In Fig. 22 one end of a longitudinal section of a polygerm is shown with the completed primary masses. Three of these masses are seen in the figure, together with a portion of a fourth. Attention should be called to the fact that the adipose tissue, although in contact with the polygerm, is still a distinct structure. In the process of forming the primary masses not all of the elements of the nucleated membrane are taken into these structures. Some of them are left behind and later lie in the inter-embryonal spaces or interstices. In Fig. 22 a number of these elements (cells and nuclei) are shown at the point marked "N," lying between the primary masses and the adipose layer.

In another portion of the same polygerm a single primary mass is being constricted off laterally. It appears as a bud extending from the main body of the polygerm. It is such cases

as this which give rise to the condition frequently seen in whole mounts, in which the surface of the polygerm displays many protuberances.

(f) *Formation of the Secondary Masses.*—The primary masses soon become broken up into secondary masses. This is also brought about by constrictions of the nucleated membrane (Fig. 23). These secondary masses may contain more than one embryo, in which case they immediately form constrictions which result in producing still smaller masses, each of which contains a single embryo.

In the constrictions which lead to the cutting off of a single embryo with its involucre, some of the precipitated material is enclosed between that portion of the granular layer which is in contact with the embryo and that part lying adjacent to the inner surface of the nucleated membrane. These two parts of the granular layer then fuse, forming a single involucre in which are the spaces containing the precipitated material (Fig. 24). The embryo is thus surrounded by two involucre, a granular layer, and a nucleated membrane (Fig. 26). In some cases the precipitated material may be so abundant as to form a solid zone between the inner and outer parts of the granular layer; in others it is small in amount and gives the appearance of much flattened nuclei lying within this layer (Fig. 26, *P.M.*).

(g) *The Inter-embryonal Substance.*—At the close of the formation of the single embryonic masses and their involucre the inter-embryonal interstices are already filled with a substance derived from several different sources. It consists of a plasma-like matrix in which are embedded cells and nuclei. We have already noted that during the formation of the primary and secondary masses some of the elements from the nucleated membrane are not included in the outer involucre, but are left in the inter-embryonal spaces. During the early history of the inter-embryonal substance, it consists mainly of product from this membrane. Later cells from two other sources enter into its formation. First, leucocytes from the host are found embedded in the matrix. They are especially abundant in those regions of the polygerm exposed directly to the body cavity, that is near a surface barren of adipose tissue. Second, fat cells

from the adipose layer invade the inter-embryonal spaces. The fat cells are the last elements to enter the inter-embryonal substance. In Fig. 13 a wedge-shaped mass of fat tissue is seen lying between the embryos in the middle region of the polygerm, on the upper side. Perhaps it would be more correct to say that the embryos bud out into the adipose tissue. Thus in Fig. 24 a single primary mass has been budded off into the adipose tissue.

The final condition of the polygerm at the end of the formation of the inter-embryonal substance is shown in Fig. 16. The adipose tissue has invaded the inter-embryonal substance from all sides of the polygerm and has become an organic part of this substance. The fat body and the included polygerm become an extremely complex structure, which may be called the *polygermal mass*.

## 2. *Dissociation of the Polygermal Mass.*

The setting free of the larval parasites into the body cavity of the host is brought about through the dissociation or disintegration of the inter-embryonal substance. The fat brought into close contact with the embryos by the invasion of the adipose tissue is digested and absorbed by them. It is therefore the first component of the inter-embryonal substance to disappear. That the fat is digested and consumed by the embryos is evidenced by the fact that the numerous other fat bodies remain intact during this period. The disappearance of the fat leaves the embryos loosely held together by the plasmalike matrix, which in turn soon disintegrates, freeing the larvæ.

The first larvæ to be set free are those situated at the periphery of the polygermal mass. Such larvæ are usually the largest present in the mass. As the inter-embryonal substance slowly disintegrates the remainder of the larvæ are gradually set free (Fig. 17). The earliest date at which free larvæ have been found was July 19; the latest, July 31. In the vast majority of cases the mass dissociates during the last week of July.

The larvæ retain the involucre for some time after being set free (Fig. 18). Once free in the body cavity they proceed to devour the contents of the host, first consuming the fat tissue, and finally the various organs. The last internal organ to disappear is the intestine.



### 3. *Pupation, and the Emergence of the Imagines.*

Pupation in *Copidosoma* occurs during the first ten days of August. The pupa stage lasts twenty-eight days. As stated above, the larvæ destroy all of the internal organs of the host, and consume such portions as are dissolved by the action of their salivary secretions. The undissolved portion consists largely of the chitinous parts of the tracheæ. The larvæ also destroy all of the body wall except the superficial layer of chitin. During the process of pupation the non-digested content of the caterpillar hardens and forms the thin-walled, oval chambers in which the parasitic larvæ lie and in which they undergo their transformation into pupæ. The superficial layer is perfectly transparent, and at first is very flexible. Later, as drying occurs, it shrinks in on the walls of chambers and becomes hard and rigid, the whole forming the typical mummified carcass (Figs. 2, 4, 6). Practically all of the pupæ are oriented in a definite fashion in the carcass. Their heads are directed toward the anterior end of the carcass. Just before becoming immobile, the *Gnorimoschema* larva almost invariably turns the head upward in the gall chamber; likewise, the parasitic larvæ, just before pupating, orient themselves so that their heads are directed upward, in the direction of the anterior end of the carcass.

The imagines come out during the last week of August and the first week of September (Table I.). They escape by gnawing holes through the walls of the chambers and the superficial chitinous layer, both of which become very fragile. As a rule they all emerge practically at the same time. Several cases have been observed in which the entire brood has escaped within a period of ten minutes.

Once free from the carcass, they immediately gnaw a hole through the wall of the gall. Their escape is greatly facilitated by the habit of the caterpillar, just before becoming immobile, of eating out a passage-way to, or nearly to the epidermis of the plant. But in no case does the parasitized caterpillar secrete a silken plug. Hence, in order to escape to the exterior, the parasites have only to cut through the remaining thin portion of the wall.

The parasites must winter over in the imago state; otherwise

they would not be able to parasitize the normal or spring eggs of *Gnorimoschema*. Copulation, however, takes place immediately after the adults emerge, but the females do not parasitize the

TABLE II.

TABLE SHOWING VARIATION IN LENGTH OF LARVÆ IN THREE LOTS OF COPIDOSOMA.

Length in Lines.	Lots.			Length in Lines.	Lots.		
	I	II	III		I	II	III
1				29		3	3
2				30		10	7
3			2	31		3	1
4			3	32	I	5	
5			10	33		1	1
6		3	14	34		2	3
7			13	35		4	3
8		I	12	36		2	1
9			4	37		8	5
10		I	3	38		1	4
11		I	4	39	I	2	2
12			2	40	3	3	9
13			2	41	4	4	4
14			2	42	2	7	5
15	I		6	43	2	3	7
16	I		3	44	I	3	7
17	4	4	12	45	3	5	2
18		I	7	46	I	8	4
19	I	6	16	47	I	5	3
20		4	17	48	I	10	1
21			9	49	2	13	2
22		9	7	50		10	2
23		5	6	51		4	
24		3	4	52	2	8	
25		3	13	53		1	
26		3	5	54			
27		I	4	55	I	2	
28		4	I	56			

fall eggs of this moth. Only on one occasion has an attempt to oviposit in such eggs been observed. In this instance the few females which made the attempt were not able to penetrate the shell of the egg with the ovipositer.

#### 4. The Abortive Embryos.

One of the most interesting discoveries made in connection with the study of *Copidosoma* is what we shall call the abortive embryos or larvæ, to which brief reference has already been made. Abortive embryos occur in the development of many different species of both invertebrates and vertebrates. They

are especially common in mammals. For example, my colleague, Dr. C. G. Hartman, has found a great mortality of embryos in the development of the opossum. Degenerating embryos are found throughout the brief but entire period of gestation. Abortive embryos have been found in at least three other species which have a polyembryonic type of development. One of the two embryos which develop from a single egg of the earthworm, *Lumbricus trapezoides*, sometimes degenerates. Fernandez ('09) has observed rudimentary embryos in the South American armadillo, *Tatusia hybrida*, and I have on several occasions seen them in the blastocyst of *Tatusia novemcincta*. But in no case with which we are acquainted is their number and constancy of occurrence so striking as in *Copidosoma*.

Our attention was first attracted to these abortive embryos while dissecting out a batch of larvæ from a large caterpillar. Most of the larvæ in the lot were large and about on the point of undergoing pupation, but in addition to these large individuals, there were a number of smaller ones. At first it was supposed that two distinct species of parasitic larvæ were present, or that we had a condition similar to that described by Silvestri for *Litomastix*, of sexual and asexual larvæ. It was noted, however, that the small larvæ had the same general structure as the larger individuals, except that they still possessed the two involucre typical of all of the younger larvæ of this species.

A study of serial sections of more than a hundred polygerms has completely demonstrated beyond any possibility of doubt that the small rudimentary embryos are derived from the same egg as larger normal larvæ, and consequently do not belong to a different species. The sections show that degenerating embryos are to be found in every stage of development of the polygerm, from the time of the formation of single embryos until the larvæ are set free into the body cavity of the host. In Fig. 24 is shown a degenerating embryo which has not yet been completely cut off from its fellow by the constriction of the nucleated membrane. Its nuclei have already completely disintegrated. In Fig. 26 is another embryo well on the way to complete disintegration. Finally Fig. 17, which is a portion of a polygermal mass about at the close of dissociation, contains at least four or five rudimentary embryos. They stain darker than the normal individuals.

The degeneration of embryos or larvæ does not cease immediately after the dissociation of the polygermal mass, but such embryos are found up until the beginning of pupation. About fifty lots of free larvæ have been dissected out of caterpillars, and

TABLE III.

TABLE SHOWING THE NUMBER OF PARASITES IN FEMALE BROODS.

Brood.	No. of Individuals.	Brood.	No. of Individuals.
1	25	46	200
2	42	47	201
3	49	48	207
4	52	49	210
5	73	50	210
6	89	51	212
7	91	52	213
8	95	53	213
9	100	54	214
10	100	55	215
11	106	56	215
12	108	57	216
13	115	58	216
14	119	59	217
15	120	60	229
16	121	61	234
17	122	62	236
18	124	63	236
19	124	64	237
20	125	65	245
21	131	66	248
22	137	67	250
23	142	68	251
24	145	69	254
25	146	70	256
26	150	71	257
27	151	72	260
28	153	73	261
29	154	74	264
30	156	75	272
31	161	76	275
32	163	77	280
33	164	78	284
34	167	79	286
35	174	80	292
36	174	81	301
37	178	82	314
38	178	83	328
39	179	84	335
40	181	85	338
41	183	86	340
42	189	87	347
43	192	88	378
44	194	89	385
45	195	90	395

Total = 17,864.

Average = 198.48.

almost without exception degenerating individuals were found. During the early period of the free larval stage, any given lot will show great variation in the size of the larvæ. To show this, all of the individuals of three lots have been measured in the terms of lines on the eye-piece micrometer scale (Table II.). In Lot I. there were only thirty-two larvæ. All but six of these would have reached maturity. Lot II. contained 176 larvæ, but at least twenty of these were degenerating. Lot III. contained 257 larvæ, and probably more than a hundred of them would have degenerated eventually.

A series of sketches of these larvæ is shown in Fig. 25, *A* to *H*. The first four or five of these types would have developed to maturity, but such larvæ as those illustrated in *F* to *H* degenerate. The most common types of degenerating embryos are the small spherical or oval-shaped masses (*G*, *H*). In one extreme case the lot of embryos consisted of about thirty of these masses, together with only a single normal larva. Doubtless many other similar masses had already degenerated.

It is difficult to assign any definite cause to the degeneration of these embryos, although it probably has something to do with nutrition. In some cases it seems to be due to the fact that the division of the egg has been carried too far. Some of the primordia receive but few embryonic nuclei, and these are invariably the first to degenerate in the polygerm. In other cases the degeneration is apparently due to the lack of proper nutrition. Most of the polygerms are early surrounded by the thick layer of adipose tissue, upon which the early development of the embryos depends. But other polygerms are almost if not entirely barren of adipose cells, and it is an observed fact that the mortality of embryos in such cases is exceedingly high. In Fig. 14 one of these cases is shown. This polygerm, which is devoid of fat tissue, contains more than a hundred embryos, not more than thirty or thirty-five of which have developed normally.

#### V. NUMBER AND SEX OF COPIDOSOMA PARASITES FOUND IN GNORIMOSCHEMA.

The number of matured parasites developing in the *Gnorimoschema* larva has been determined in 162 cases. This has been

done by removing the carcass from the gall chamber a short time before the emergence of the parasites, and enclosing it in a small vial. After all of the parasites have emerged they are killed by filling the vial with 80 per cent. alcohol, and then counted under a binocular microscope. This procedure has the advantage of eliminating the possibility of contamination from other polyembryonic broods. Furthermore, the use of the binocular in counting enables one to distinguish readily the two sexes. The strong sexual dimorphism in *Copidosoma* makes this task rather easy. The females have the enlarged club-shaped,

TABLE IV.

TABLE SHOWING THE NUMBER OF PARASITES IN MALE BROODS.

Brood.	No. of Individuals.	Brood.	No. of Individuals.
1	41	32	178
2	53	33	179
3	61	34	180
4	67	35	180
5	90	36	180
6	93	37	182
7	96	38	190
8	100	39	190
9	101	40	192
10	106	41	199
11	107	42	199
12	113	43	202
13	118	44	204
14	119	45	214
15	124	46	215
16	124	47	218
17	124	48	223
18	127	49	225
19	128	50	232
20	136	51	233
21	137	52	236
22	138	53	236
23	139	54	245
24	142	55	247
25	147	56	272
26	152	57	277
27	168	58	278
28	171	59	323
29	172	60	324
30	177	61	328
31	177	62	345

Total = 19,874.

Average = 175.32.

terminal segment of the antenna, and bright yellow legs, while the males do not have the enlarged segment and the legs are of a

dark, more or less mottled color. One can therefore readily detect a mixed brood under the microscope.

The 162 broods studied were taken at random from the field, and therefore in all probability the data on numbers and sex yielded by them represent the approximate sex ratio for the species. These 162 broods contained a total of 31,001 individuals, or an average of over 191 to the brood. Ninety of these, or 55.56 per cent., contained only female parasites, 62, or 38.27 per cent., contained only male parasites, and 10, or 6.17 per cent., contained mixed broods of males and females.

There are therefore not only a larger number of female broods than male, but the average number of individuals in the former exceed that of the latter. Female broods average a little over 198 individuals to the brood (Table III.), while male broods average only about 175 (Table IV.). The range in the number of individuals in these broods (from 25 to 395 in the female, and from 41 to 345 in the male) makes it evident that these averages are of little significance, except, perhaps, to show that the fertilized egg is slightly more prolific than the unfertilized egg.

Of the total number of individuals (31,001), 63.41 per cent. are females and 36.59 per cent. males; but obviously the true sex ratio can not be based on these figures. It must be determined from the number of male and female broods. It would not be a difficult matter to determine this ratio were it not for the uncertainty of the origin of some broods. There is always the possibility in these insects that more than one parasitic egg has been laid in the egg of the host, and hence the parasites which later emerge may not constitute a true polyembryonic brood, but in fact represent two or even more such broods. Under the circumstances, the best that one can do is to determine approximately the sex ratio for the species. This can be done in the following manner. If we assume, as all previous workers have done, that each of the mixed broods is the product of at least two eggs, then, in accordance with the law of probability, we can determine the number of unmixed male and female broods, each of which must also have been produced from two eggs. Worked out on this basis, it is found that the ratio of females to males is 106/76 or a sex ratio of approximately 3 : 2

This leads to a discussion of mixed broods, and especially to a consideration of the question as to how such broods have come into existence. The obvious explanation of their origin is the one given above, viz., that they arise from two eggs. Marchal and Silvestri, who have studied the development of polyembryonic insects, both offer this explanation. They support the conclusion by citing the fact that two (or more) parasitic eggs are sometimes laid in the egg of the host. According to Marchal, such eggs develop independently, each producing a distinct polygerm and consequently a distinct brood. If the two eggs are of the same sex potentiality, the individuals developing from them will be either all females or all males, according to whether or not the eggs are fertilized or unfertilized. The dual origin of these double broods naturally elude detection in lots that have emerged. But if one of the two eggs is unfertilized and the other fertilized, the result will be a mixed brood, consisting of males and females. This conclusion of Marchal and Silvestri is strongly supported by the facts of polyembryonic development in the armadillos, in which it has been conclusively demonstrated (Fernandez, '09, Patterson, '13) that all of the embryos of a given pregnancy are the product of a single egg. As a result, mixed litters are never found in these mammals.

That mixed broods may arise from two eggs in *Copidosoma* is supported by the fact that two polygerms are sometimes found in a single *Gnorimoschema* larva. However, certain facts concerning the condition of mixed broods in this species, make it doubtful whether the origin of all such broods can be explained in this obvious way. Careful dissections of something over a hundred parasitized *Gnorimoschema* larvæ have revealed only two cases in which a single larva contained more than one polygerm. Since 6.17 per cent. of all broods are mixed, and since a similar number of unmixed broods would have a dual origin, we should expect to find over 12 per cent. of all parasitized larvæ containing two polygerms, but instead, less than 2 per cent. are found.

Another line of evidence which is not in harmony with the view that mixed broods are always the product of two or more eggs, is the great preponderance of females in certain lots. Of



the nine complete lots (Broods 2 to 10) listed in Table V., the number of females in each case is greater than the number of males. In some cases (Broods 3, 4, 5, 7, 8), this difference is not so great but that the origin of each lot can be explained on the assumption that two eggs have been deposited in the egg of the host. But in Broods 2, 6, 9, and 10 the number of females in excess of males is indeed striking, making it difficult to explain the origin of such broods on the basis of two eggs.

In view of these facts, the writer is convinced that some other explanation must be offered for the origin of certain mixed broods; in fact, one involving the idea that a single fertilized egg may give rise to a few males as well as a relatively large number of females. This would be possible on the basis of the following assumption.

TABLE V.

TABLE SHOWING THE NUMBER OF PARASITES IN MIXED BROODS.

Brood.	No. of Individuals.	Females.	Males.
1*	89	20	69
2	162	153	9
3	172	92	80
4	207	126	81
5	216	176	40
6	235	223	12
7	241	161	80
8	300	235	65
9	304	292	12
10	337	316	21
Totals.....	2,263	1,794	469
Average.....	226.3	179.4	46.9

\* This brood is not complete, owing to the fact that some of the larvæ and pupæ had been destroyed by a large dipterous larva.

If *Copidosoma* conforms to the general scheme for sex determination in insects, the females must have the 2 X chromosomes, and males the single X chromosome. Ordinarily, during the process of cleavage, all of the chromosomes in the fertilized egg divide equally, so that all of the nuclei entering into the formation of the embryos will carry the XX chromosomes, thus producing a brood of females. But if during the early development of the egg it should happen that the two X chromosomes in one or more cleavages should not divide but separate, one going to each pole of the spindle, each daughter nucleus would then receive a single

X chromosome. If such nuclei later divided in the typical manner and gave rise to embryos, such embryos would be males. One is encouraged to make this suggested explanation in the light of Bridges' ('13) discovery of the non-disjunction of the sex chromosomes in *Drosophila*. In *Copidosoma* the separation of the sex chromosomes during cleavage would be a case of "somatic" or "cleavage disjunction," while in *Drosophila* these chromosomes fail to separate or "disjoin" in the reduction division of the egg.

In conclusion attention should be directed to the frequency of *Copidosoma* in nature. At Woods Hole about twenty per cent. of all *Gnorimoschema* larvæ are infected with this parasite

TABLE VI.

TABLE SHOWING PERCENTAGE OF PARASITIZED CATERPILLARS IN THE GALLS OF  
SOLIDAGO SEMPERVIRENS.

Number of Galls.	Date.	Parasitized by <i>Copidosoma</i> .	Normal Galls	Empty.	Parasitized by Other Parasites.
9	7-29-12	7	2	0	0
33	8- 5-12	5	15	0	13
33	8-17-12	9	16	5	3
56	8- 8-12	7	26	10	13
29	8-12-12	8	16	0	0
141	8-25-12	20	56	33	32
14	7- 7-13	1	13	0	0
16	7-14-13	0	13	0	0
39	7-15-13	8	31	0	0
38	7-19-13	4	*	*	*
23	7-23-13	2	20	0	1
38	7-26-13	6	*	*	*
27	8- 5-13	4	*	*	*
24	8-25-13	4	17	3	0
18	6-15-14	2	14	2	0
19	6-18-14	3	16	0	0
43	6-22-14	19	19	3	2
40	6-24-14	9	20	10	1
20	7-16-14	1	19	0	0
24	7-30-14	0	21	0	3
25	7-23-15	3	12	7	3
18	7-26-15	5	11	0	2
66	7-30-15	25	37	2	2
35	8- 4-15	14	35	1	6
Totals. . 828		166			

\* Record incomplete. About 20 per cent. of the caterpillars are parasitized by *Copidosoma*.

(Table VI.). As may be seen from the table, the extent of infection varies greatly in the lots of galls taken from different regions (those collected on a given date are all from a single locality). Plants which grow in exposed places, as along the

roadside or barren spots, carry a higher percentage of galls than do those which are located in protected regions. Likewise, the moth larvæ from the galls of the former are more highly parasitized.

#### SUMMARY.

1. *Copidosoma gelechiae*, which is a parasite in the Solidago Gall Moth, *Gnorimoschema salinaris*, has but one generation a year.

2. The egg of this parasite is probably laid during the month of May.

3. The type of development in *Copidosoma* is polyembryonic. The number of individuals average about 191 per brood.

4. In the youngest stages secured the process of division of the egg into embryonic primordia is already in progress. The young polygerm consists of two distinct regions: (1) An outer zone, or nucleated membrane, containing the free polar nuclei; (2) a central region, containing the true embryonic nuclei.

5. The embryonic nuclei segregate into groups, which become surrounded by a dense layer of granular protoplasm and form the primordia of the multiple embryos.

6. During early growth the polygerm elongates into a cylindrical-shaped structure, which becomes broken up into several spherical, primary masses by the formation of constrictions in the nucleated membrane. Each primary mass receives several of the primitive embryos.

7. The primary masses become broken up into secondary masses by further constrictions of the nucleated membrane. At the end of these divisions, each embryo is separated from the others and is surrounded by an inner and an outer involucre—the former derived from the granular protoplasm and the latter from a portion of the nucleated membrane.

8. The interstices between these masses become filled with an inter-embryonal substance derived from at least three sources: elements from the nucleated membrane, leucocytes, and cells from the adipose tissue, which usually is laid down in the form of a thick layer on the outer surface of the polygerm. The entire structure thus becomes a complex, which may be called the polygermal mass.

9. The dissociation of the inter-embryonal substance sets the larvæ free in the body cavity of the host. This occurs during the last week of July.

10. Abortive or degenerating embryos are found throughout the entire period covered by the polygerm and free larval stages.

11. The free larvæ destroy the entire contents of the caterpillar, except the chitinous parts of the tracheae, and leave only the superficial layer of chitin of the body wall intact. The detritus left in the larval chitin hardens to form thin-walled, oval chambers in which the larvæ lie and undergo pupation. The superficial layer of chitin also hardens, and the larval skin thus becomes transformed into the typical mummified carcass, filled with the parasitic pupae.

13. Pupation takes place during the first ten days of August and lasts about a month.

14. The number of adult parasites emerging from the carcasses varies from 25 to 395. There is a preponderance of females, about 55 per cent. of all broods being females. Furthermore, the average number of females emerging from a single carcass is 198 as compared with 175 for the males. Ten mixed broods of males and females have been obtained. Some of these have doubtless arisen from two or more eggs; but it is suggested that such broods may also arise from a single fertilized egg, by a process of disjunction of the sex chromosomes during the early cleavage stages.

WOODS HOLE, MASS.,

August 12, 1915.

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## DESCRIPTION OF PLATES.

## PLATE I.

FIG. 1. A typical gall of *Gnorimoschema salinaris*, Busck, situated at the base of the stalk of the swamp goldenrod, *Solidago sempervirens*.  $\times \frac{1}{4}$ .

FIG. 2. Gall cut open to show the position of the mummified carcass of *Gnorimoschema*. Natural size.

FIG. 3. Gall cut open and carcass removed to show the shape of cavity. Note that the walls of the cavity are smooth and that the excrement from the caterpillar is packed in the bottom of the cavity. Natural size.

FIG. 4. Mummified carcass from gall shown in Fig. 3. Natural size.

FIG. 5. Lepidopterous larva which is an inquiline in the gall of *Gnorimoschema*. Note the irregular shape of the cavity which contains scattered trash and excrement. Natural size.

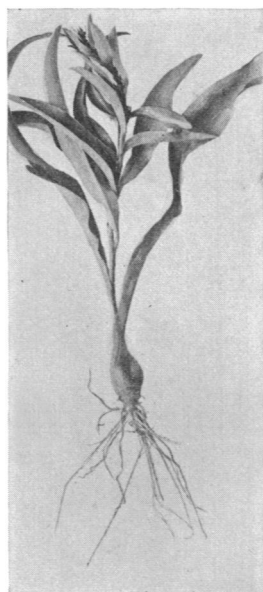
FIG. 6. This gall shows an incomplete passage-way, lying just above the head of the carcass. Normal size.

FIG. 7. Side view of a gall showing the orifice of the passage-way, closed by silken plug. Natural size.

FIG. 8. Stalk of swamp goldenrod containing two galls.  $\times \frac{1}{4}$ .

FIG. 9. Gall containing a non-parasitized caterpillar. Natural size.

FIG. 10. Gall containing a parasitized caterpillar. Natural size.



1



2



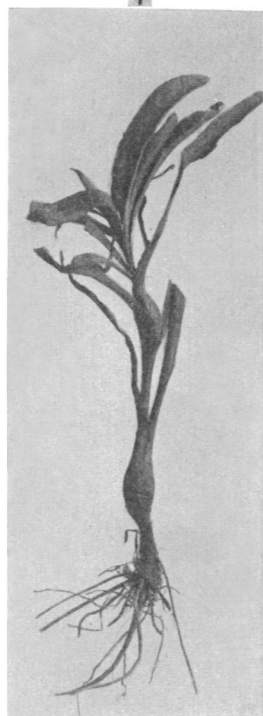
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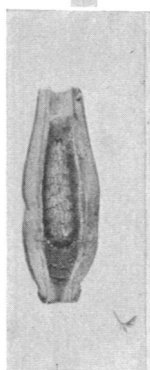
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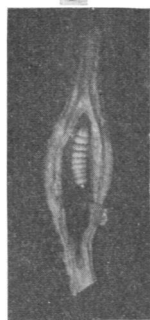
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6



7



9



10

## PLATE II.

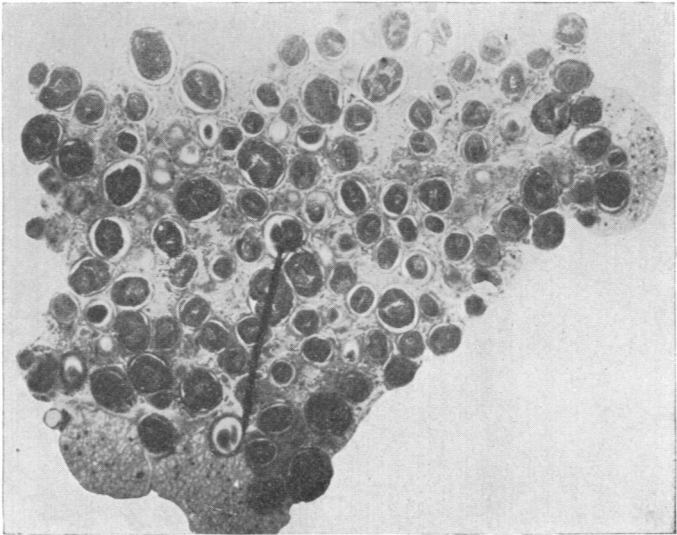
FIG. 11. Photomicrograph of a section of an irregular polygermal mass.  $\times 40$ .

FIG. 12. Photomicrograph of a single embryo from mass shown in next figure.  $\times 180$ .

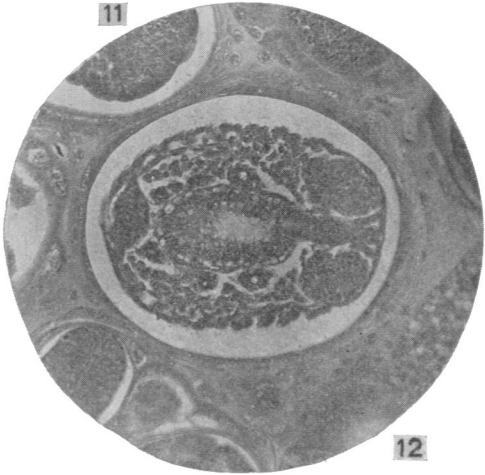
FIG. 13. Photomicrograph of a longitudinal section of a flat, plate-like polygermal mass.  $\times 40$ .

FIG. 14. Photomicrograph of a spherical polygermal mass which is barren of adipose tissue.  $\times 40$ .

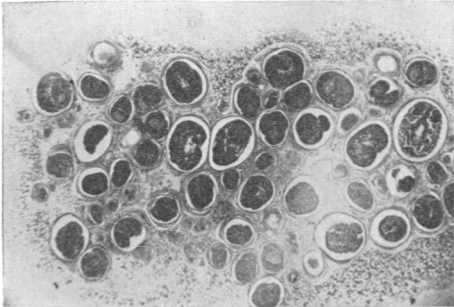




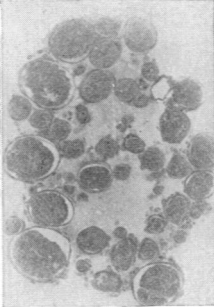
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## PLATE III.

FIG. 15. Photomicrograph of the middle portion of longitudinal section of a small caterpillar. A fat body containing a polygerm lies just below the intestine.  $\times 44$ .

FIG. 16. Photomicrograph of a portion of a section of a polygermal mass which was about to begin disintegration.  $\times 44$ .

FIG. 17. Photomicrograph of a section of a polygermal mass undergoing dissociation.  $\times 44$ .

FIG. 18. Photomicrograph of a mass of free larvae from the body cavity of the caterpillar. Note that each embryo is still surrounded by the involucre.  $\times 44$ .

*Reference Letters Used in Plates IV.-VI.*

*A.E.*, Abortive Embryo.

*A.T.*, Adipose Tissue.

*C.*, Clear space left by contraction of  
Precipitated Material.

*E.N.*, Embryonic Nuclei.

*G.L.*, Granular Layer.

*I.I.*, Inner Involucre.

*I.S.*, Inter-embryonal Substance.

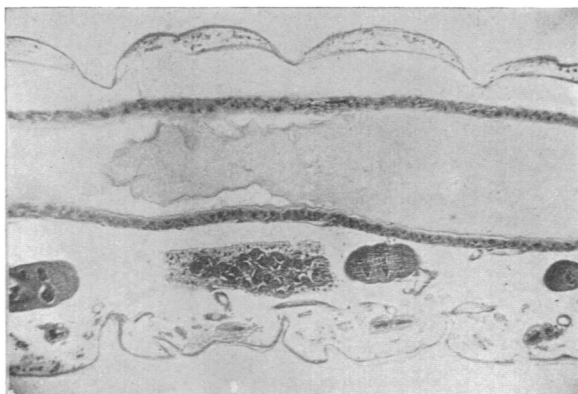
*N.M.*, Nucleated Membrane.

*O.I.*, Outer Involucre.

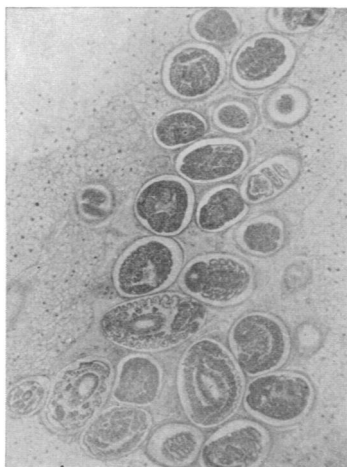
*P.D.*, Primary Division of polygerm.

*P.E.*, Primitive Embryo.

*P.M.*, Precipitated Material.



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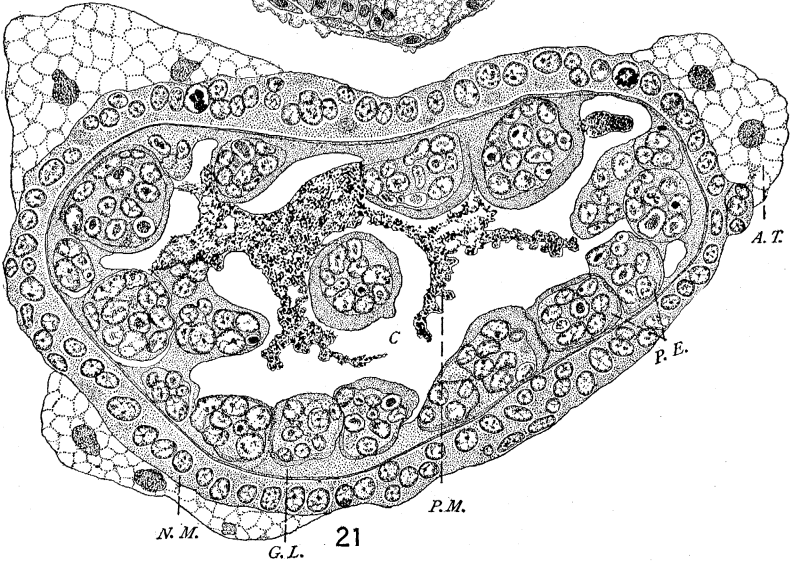
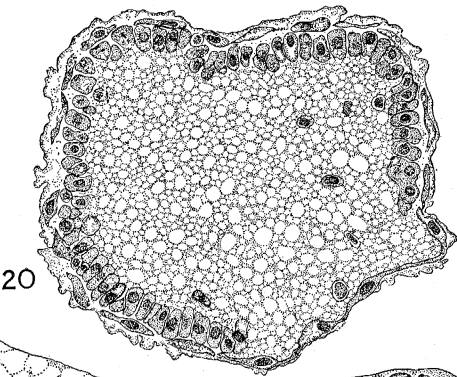
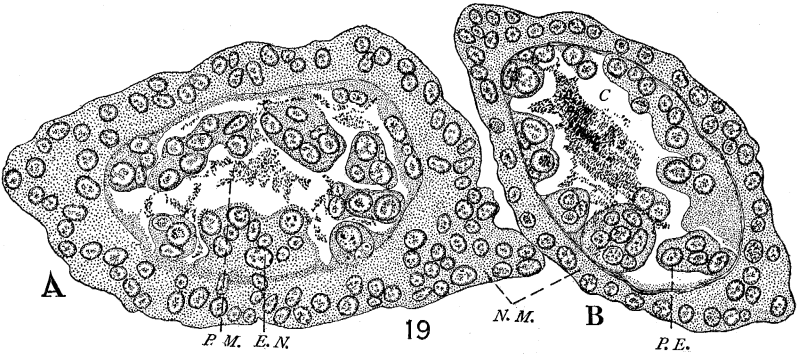
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## PLATE IV.

FIG. 19. *A* and *B* longitudinal sections of two polygerms lying close together in the same caterpillar. These polygerms show an early phase of the segregation of the embryonic nuclei to form the separate embryos.  $\times 489$ .

FIG. 20. Section of an egg of *Gnorimoschema* which has started to develop parthenogenetically.  $\times 173$ .

FIG. 21. Longitudinal section of a polygerm showing the end phase of embryo formation.  $\times 480$ .

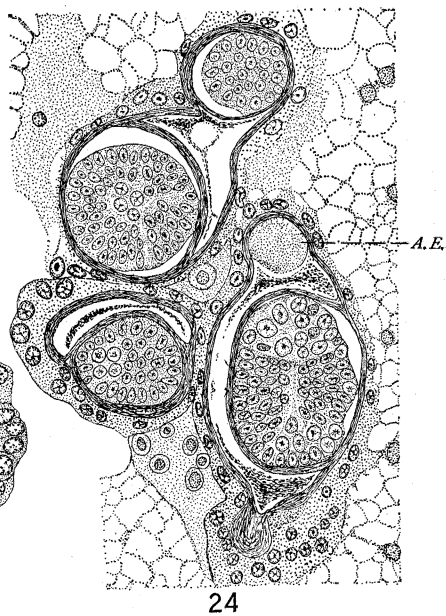
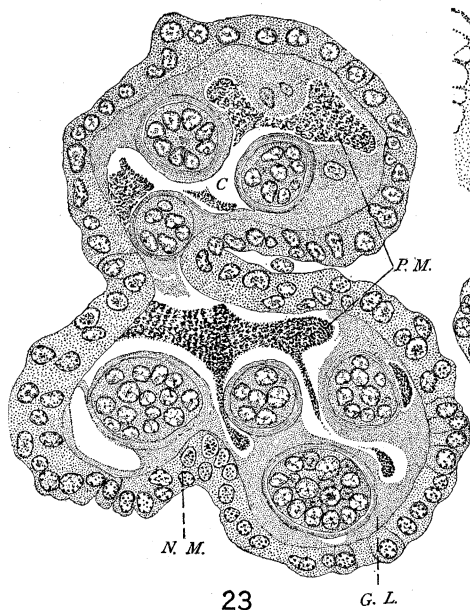
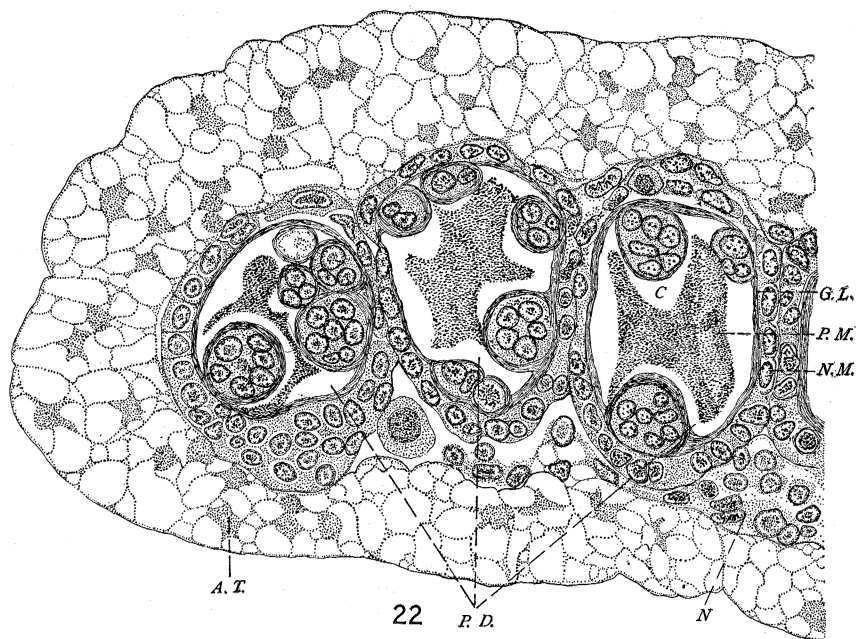


## PLATE V.

FIG. 22. One end of a longitudinal section of a polygerm showing three of the twelve primary divisions into which it has been divided by constrictions of the nucleated membrane.  $\times 373$ .

FIG. 23. Section of a primary mass showing the process by which it is further divided up into secondary masses by constrictions of the nucleated membrane.  $\times 508$ .

FIG. 24. Section of a single isolated, primary mass about at the close of its division into single embryonic masses.  $\times 257$ .

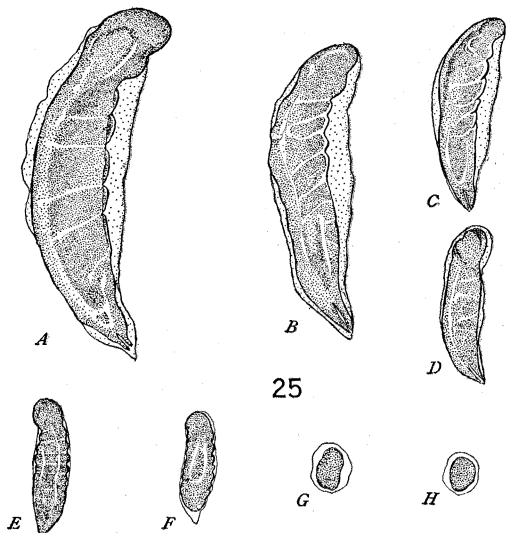


## PLATE VI.

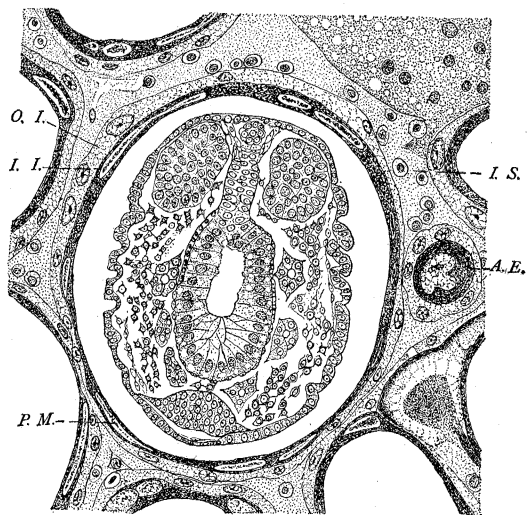
FIG. 25. *A* to *H*, Series of sketches from Lot III of the free larvae listed in Table III. This figure shows the great variation in size of the larvae from a single caterpillar. They are all drawn to the same scale.

FIG. 26. Detailed drawing of a section of one of the embryos seen in Fig. 13. It shows the relation of the inter-embryonal substance and involucre to the embryo.  $\times 187$ .





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